THE RELATION OF BLOOD OXYGEN TRANSPORT TO RESISTANCE TO ANOXIA IN CHICKS AND DUCKLINGS ¹

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The relatively greater resistance of the new-born and young animals to complete anoxia in comparison with that of the adult animal has been studied by Himwich et al. (1941) who have advanced the hypothesis that differences in the aerobic and anaerobic energy release in the young and adult brains are the probable cause of the differences in resistance to anoxia. The newborn and young of many species of animals have been exposed to 100 per cent No. He, and COo and have proved to be remarkably resistant to complete anoxia in comparison to older individuals of the same species (Fazekas et al., 1941). Since there is a total lack of oxygen in the blood stream under conditions of total anoxia and since the brain is the organ most susceptible to anoxia the oxygen requirement of the brain of newborn and young animals has been studied in comparison to the energy requirement of the brain of older animals of the same species in order to find some possible basis for the greater resistance of the young and newborn to anoxia. Himwich et al. (1941) and Chesler and Himwich (1944) have demonstrated that the anaerobic energy release in the brain of the newborn is relatively greater, in proportion to the total energy requirement of the brain, than in older individuals of the same species. After birth there is a rapid increase in energy requirement as measured by the amount of respiration carried on in the brain (Tyler and von Harreveld 1942). This increase is met, chiefly, by increase in the aerobic energy release. In the newborn the total energy requirement is low and a relatively larger proportion of the requirement is met by anaerobic energy release. The survival of the newborn and young under conditions of total anoxia is adequately explained on the basis of the relatively great anaerobic energy release in the brain of the young and newborn compared to the total energy required by the brain at this stage of development to maintain the functional integrity of the organism.

Although Quastel and Wheatley (1932) demonstrated differences in the energy requirement of surviving brain slices of cat and rat brains—the rat brain had a higher energy requirement as evidenced by greater oxygen consumption of surviving brain slices—the possibility remains that in the adult animal species differences in survival at high altitude under conditions of incomplete anoxia may be explained, in part, on several bases beside differences in brain metabolism. One of these factors is differences in oxygen transport by the blood.

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Rostorfer and Rigdon (1945) were able to show that malarial infection greatly reduced survival time of ducks and chicks at simulated high altitude. The effect of a severe malaria infection on the survival time was marked by the third day after the birds had been inoculated with the malarial organism. At this time there was only a small percentage of red cells infected, but a shift in acid-base balance and a reduction in the oxygen carrying capacity were developing. In the study of the effect of malaria on survival of birds at high altitude a specific difference in resistance to high altitude anoxia between ducks and chicks was reported. This difference in resistance was still evident on the third day after inoculation with malaria, although there was decreased resistance in each case.

These earlier experiments suggested to the authors that specific blood differences might be related to the specific resistance to anoxia in the case of young ducks and chicks. Accordingly, a study was made of the oxygen capacities, the oxygen dissociation curves, the amounts of hemoglobin present in blood of young and adult ducks and chickens in relation to their resistance to anoxic anoxia.

MATERIALS AND METHODS

White Pekin ducks and chicks of mixed breed, obtained from a commercial hatchery, between 3 and 21 days old were subjected to continuous decompression until convulsions and death occurred in a decompression chamber as previously described by Rostorfer and Rigdon (1945). Five to ten birds of the same age and species were observed during one decompression. In all experiments the rate of decompression was approximately the same with only a slight variation. The rate during the first four minutes of simulated ascent was between 1,700 and 1,800 feet per minute, between 700 and 900 feet per minute during the next 15 minutes, and 400 feet per minute during the next 40 minutes. After reaching a simulated altitude of 38,000 feet the rate of climb was such that during the next 12 minutes the altitude increased to only 40,000 feet. The altitude was recorded every 4 minutes during the decompression. These data were plotted against time and the total area under the resulting curve up to the time of death of the bird was calculated for each bird. The total area under the curve may be taken to represent the resistance of the bird to anoxia. The unit of resistance was expressed as the altitude in feet times the duration in minutes and was expressed as foot-altitude minutes.

Ducklings and chicks in groups of 7 to 12 individuals the same age were placed in the tank and decompressed until they were dead in the manner described. The ages of the various groups were 3, 6, 10, 15, and 20 days old. The average resistance to incomplete anoxia at simulated high altitude was obtained by analysis of data found by decompressing several age-groups of birds of each species. The number of birds in each separate decompression was determined by the size of the individuals.

Blood samples were obtained by heart puncture from 3 to 4 ducks or 6 to 12 chicks of the same age and pooled. Coagulation was prevented by adding 1 ml. of a 1 per cent solution of the sodium salt of heparin to each 9 ml. of blood. All red cell counts and hemoglobin and gas analyses were carried out on the pooled samples.

Oxygen capacities were determined by analysis of blood equilibrated in Barcroft tonometers with air at 38° C. Analyses were made by means of the Van Slyke manometric apparatus.

Oxygen dissociation curves were calculated for the pooled samples by equilibrating blood at a constant CO₂ tension of 31 mm. Hg and at varying oxygen tensions. Three gas mixtures were used containing 3.4, 7.44, and 11.86 per cent oxygen which corresponded to oxygen tensions of 24 ± 0.5 , 53 ± 0.5 , and 83 ± 0.5 mm. Hg, respectively. Analyses carried out on blood equilibrated at these three oxygen tensions gave data from which the oxygen dissociation curves were calculated by the use of the formula $y = \frac{100 \ K_{\perp} n}{1 + K_{\perp} n}$, when the oxygen capacity of the blood was known (Hill, 1910).

Hemoglobin determinations were made on each pooled sample by the use of the Schulte and Elvehjem (1934) colorimetric method. Hemoglobin was determined, also, by calculation from the oxygen capacity. These data indicate the amount of functional hemoglobin.

Cell counts were made in the usual manner on the pooled blood and the color indices were calculated by dividing the grams of hemoglobin calculated from the oxygen capacity by the total red cell counts.

Results

In order to determine the specific resistance of young and adult ducks and chickens to the incomplete anoxia produced at simulated high altitude a series of decompression experiments were carried out in the manner described. The data represented by Figure 1 show the decreasing resistance to anoxia with increasing age. The three-day old birds of both species had the greatest resistance. There appeared to be no change in resistance between the 15- and 20-day old birds in either species. There was, however, definitely greater resistance in the duck than in the chick at all ages compared. Adult birds were not studied but there are reasons to assume that the adult duck would be more resistant to anoxia than the adult chicken.

These data indicate that the newly hatched and young birds of the same species are more resistant to incomplete anoxia produced at simulated altitude. This corresponds to the resistance of young and newborn mammals studied by Himwich and others. The data indicate, also, a specific difference in resistance to incomplete anoxia between ducks and chicks. Ducks 20 days old decompressed in the usual manner succumbed at altitudes between 34,000 and 36,000 feet, while chicks 20 days old were all dead at 27,000 feet when the decompression was at the same rate as that for the ducks.

There is little doubt that specific differences in oxygen capacity and color index exist among animals. This difference might possibly bear some relation to resistance to anoxia. The oxygen capacities and color indices were determined for all blood samples. Determination of oxygen capacities of duck and chick blood revealed that the duck blood had considerably greater oxygen capacity. Duck blood from 20-day old birds had an average oxygen capacity of 12.27 volumes per cent. Chick blood from birds the same age averaged only 10.47 volumes per cent.

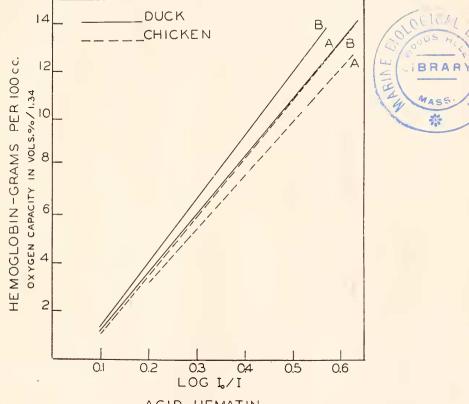
The color indices of the 20-day old duck varied around 3.6×10^{-11} . Rostorfer and Rigdon (1946) found that the color indices gradually increased with age of the young ducks. The color index of chicken blood is approximately 3.1×10^{-11} and there seemed to be no increase in the color index with age as in the duck. The color index of blood taken from the adult chicken was 3.3×10^{-11} . There was an appreciable difference in total red cell counts between the duck blood and the chick blood. The average count for the pooled blood of the chick was 2.2 million and the average count of the pooled blood of the duck was 2.6 million per cubic millimeter.

The chick blood in comparison to the duck blood had fewer red cells, decreased color index, and lower oxygen capacity.



FIGURE 1 is a graphic representation of the data on the study of relative resistance of chicks and ducks to simulated altitude. Resistance is expressed in feet of altitude times the duration at altitude in minutes. Each age group represents the average data of 10 to 20 ducks or chicks.

A considerable difference between the amount of hemoglobin determined colorimetrically and that calculated from the oxygen capacity was found for young and adult ducks by Rostorfer and Rigdon (1946). A similar study was carried out on young and adult chicks. The comparison is made in Figure 2 which represents the relationship between the amount of hemoglobin determined colorimetrically and the amount of hemoglobin calculated from the oxygen capacity. The linear expression was obtained by determining the amount of hemoglobin colorimetrically and by calculation from the oxygen capacity of a diluted, a normal, and a concentrated sample of the same pooled blood. Cell counts of the three samples, dilute, normal, and concentrated, were made and the color index of each determined. There was usually close agreement between the color indices of the three samples. The young chicks and ducks carry less oxygen per gram of hemoglobin than the adults based on the colorimetric hemoglobin. There was a slower shift toward the adult relationship with increasing age in the duck than in the chick. Thirty-day old chicks were found to have hemoglobin which corresponded to that found in the hen. The linear relation between oxygen capacity and the acid hematin of the adult chicken blood was the same as that of the young duck.



ACID HEMATIN

FIGURE 2 is a graphic representation of the relationship of the amounts of hemoglobin calculated from the oxygen capacity in comparison to the amount of hemoglobin determined by photo-electric colorimetry in the blood of young (A) and adult (B) domestic ducks and chickens.

The equilibrium between hemoglobin of bird blood and oxygen at various oxygen tensions has been investigated by Wastl and Leiner (1931) whose work indicated that blood of the duck and of the pigeon does not have typical oxygen dissociation curves. Redfield (1933) points out that such curves for blood containing hemo-globin had not been described previously but were characteristic of the blood of invertebrates. Christensen and Dill (1935) were not able to confirm the work of Wastl and Leiner, but found that the blood of ducks and other birds developed equilibria between hemoglobin and oxygen in the classical manner except at very low oxygen tensions. This discrepancy they attributed to a systematic error of equilibration. Rostorfer and Rigdon (1946) found considerable difference be-

tween the dissociation curves for young and adult ducks. The blood of the adult birds gave a typical sigmoid curve while that of the young ducklings had a greater oxygen uptake at lower oxygen tensions than would be indicated by calculation from points of equilibrium at higher oxygen tensions. However, the deviation was slight.

Bloods of young and adult chickens were investigated in similar manner. Figure 3 compares the oxygen dissociation curves of adult ducks and chickens. There was a considerable difference between the oxygen uptake of the blood of the

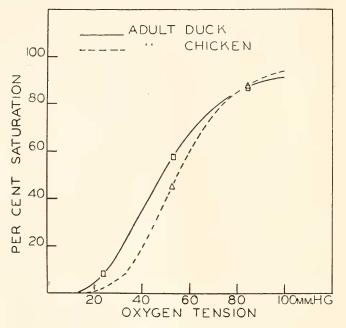


FIGURE 3 compares the oxygen dissociation curves for the adult duck and chicken at a CO₂ tension of 31 mm. Hg.

adult duck and the adult chicken at various oxygen tensions. The adult duck blood had about the same percentage of saturation at ordinary oxygen tensions but was capable of carrying a larger amount of oxygen than chick blood at low oxygen tensions.

Figure 4 compares the dissociation curves of the blood of the adult and of the young chicken. Although the curve for the blood of the young chick represents the data obtained from one sample of pooled blood only, it is reasonable to assume that it is representative. In general, the blood of the young chick appeared to have a greater percentage of saturation at all levels of oxygen tension than the blood of the adult clucken. In contrast to the blood of the adult duck, the blood of the young chick had a higher percentage of oxygen saturation at higher oxygen tensions but a slightly lower per cent of saturation at low oxygen tensions.

In general, the blood of the duck in comparison to chicken blood had greater oxygen capacity, contained more functional hemoglobin, and showed less discrepancy between the colorimetric hemoglobin and the hemoglobin calculated to be present from the oxygen capacity. Duck blood had a larger number of cells and a higher color index than chicken blood. The chemical behavior of duck blood in comparison to chicken blood, as regards the oxygen dissociation curves, indicated that the duck blood would be more efficient in the transport of oxygen under conditions of incomplete anoxia. The blood of the duck in comparison to that of the chick would appear to be more capable of maintaining the brain and other vital organs in a viable condition for a longer time under conditions of simulated high altitude and resulting anoxia.

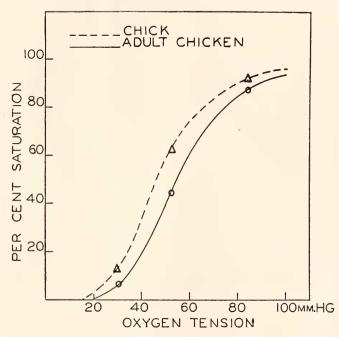


FIGURE 4 compares the oxygen dissociation curves of young and adult chicken blood at a CO₂ tension of 31 mm. Hg.

It is not unreasonable to assume that some of the difference in specific resistance to anoxia of the duck and the chick is caused by the greater efficiency of the blood of the duck at low oxygen tensions. However, a study of the anaerobic and aerobic energy release compared to the total energy requirement of the brain of the two species in question has not been made as yet. One might well assume that there are specific differences in brain metabolism.

SUMMARY

A study of the resistance of ducks and chicks to incomplete anoxia produced at simulated altitude is reported. The newly-hatched and young birds had greater resistance than older birds. The duck was found to be more resistant than the chick to incomplete anoxia at all ages studied. A study of the oxygen carrying capacities, total red cell counts, color indices, the amount of hemoglobin, and the oxygen dissociation curves of the blood of the duck and the chick is reported.

The blood of the duck has greater oxygen capacity, higher total red cell count, higher color index, more hemoglobin and a higher percentage of saturation of the blood with oxygen at low oxygen tension when compared with blood of the chicken.

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